

## CONDITIONING OF APPETITIVE AND CONSUMMATORY SEXUAL BEHAVIOR IN MALE JAPANESE QUAIL

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Two different types of stimulus objects, a live female quail artificially adorned with bright orange feathers and an inanimate toy dog, served as conditioned stimuli. For subjects in experimental groups, the conditioned stimuli were presented shortly before access to a sexually receptive normal female quail. For subjects in control groups, exposure to the conditioned stimuli was unpaired with copulatory opportunity. Subjects in the experimental but not in the control groups quickly came to approach the location of the conditioned stimulus objects. When an adorned female quail served as the conditioned stimulus, the conditioned approach behavior was controlled by a combination of the presence of the orange adornments and the visual cues of the head and neck of the female bird, and the approach behavior persisted as the adorned female moved to new locations. When the toy dog served as the conditioned stimulus, the conditioned approach behavior was limited to the spatial cues that surrounded the toy dog during conditioning trials. Although both types of stimulus objects evoked conditioned approach behavior, only the adorned female stimulus supported copulatory behavior. This last finding indicates that copulatory behavior can become redirected toward novel stimuli as a result of conditioning, but only under special circumstances. The results are consistent with the suggestion that appetitive components of reproductive behavior are more susceptible to conditioning than consummatory components. Possible reasons for this are discussed, together with implications of the results for the contribution of conditioning processes to sexual selection.

*Key words:* sexual behavior, sexual conditioning, appetitive behavior, consummatory behavior, aesthetic traits, sexual selection, Japanese quail

Reproductive behavior is central to the evolutionary biology of organisms. Studies have documented various forms of learning in reproductive behavior systems (see Domjan & Hollis, 1988, for a review). Some investigators have focused on sexual imprinting—the effects of early social experience on subsequent mate choice (e.g., Bateson, 1978; Immelman, 1972). Others have employed access to male or female partners as reinforcers in instrumental conditioning procedures (e.g., Bermant & Westbrook, 1966; Gilbertson, 1975; Sevenster, 1973; Sheffield, Wulff, & Backer, 1951). Learning in reproductive behavior systems has also been investigated using Pavlovian conditioning procedures. Odors paired with access to female conspecifics have been shown to become capable of eliciting increased ultrasound vocalizations in male mice (e.g., Maggio, Maggio, & Whitney, 1983), shorter latencies to initiate

copulation in male rats (Zamble, Hadad, Mitchell, & Cutmore, 1985), and anticipatory testosterone and luteinizing hormone secretions in male rats (Graham & Desjardins, 1980). Visual cues associated with a conspecific of the opposite sex have been shown to elicit a fin-erection response and to facilitate copulatory behavior in blue gouramies (Hollis, Cadieux, & Colbert, in press), and localized visual cues associated with a female quail have been shown to elicit conditioned approach behavior and to reduce the latency of copulatory behavior in male Japanese quail (Domjan, Lyons, North, & Bruell, 1986).

Reproductive behavior may be viewed as a sequence of responses starting with search, identification, and approach of a potential sexual partner and ending with sexual contact or copulatory responses. Early components of the behavioral sequence may be referred to as *appetitive*, and late components may be referred to as *consummatory*. Appetitive responses have been characterized as variable, plastic, and purposive, whereas consummatory responses have been characterized as rigid, simple, and “automatically discharged” (Eibl-Eibesfeldt, 1970; Tinbergen, 1951). This perspective im-

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This research was supported by Grant 39940 from the National Institutes of Mental Health. We wish to thank Robert Morter, John Barry, and Jenn Yu Liu for their technical assistance. Requests for reprints should be addressed to M. Domjan, Department of Psychology, University of Texas, Austin, Texas 78712.

plies that appetitive components of sexual behavior may be more susceptible to modification by conditioning than consummatory sexual responses.

The present experiments explored conditioning of both appetitive and consummatory sexual responses in male Japanese quail. The appetitive response we measured was approach. Consummatory or copulatory behavior in male Japanese quail consists of the male grabbing in its beak the back of the female's head or neck, mounting the female's back, and then arching its back so as to bring its cloaca in contact with that of the female (Wilson & Bermant, 1972). We measured consummatory sexual behavior by recording occurrences of each of these sexual contact responses.

The grab, mount, and cloacal contact responses involve interactions with a three-dimensional stimulus object. Previous studies of sexual conditioning have used olfactory or visual conditioned stimuli that could not be grabbed or mounted. In contrast, complex three-dimensional stimuli were used as conditioned stimuli in the present experiments. In Experiments 1 and 2, the conditioned stimulus was provided by a female quail that was made to appear highly aberrant by the addition of large bright orange feathers. In Experiments 3 and 4, the conditioned stimulus was provided by a bright yellow toy dog.

## EXPERIMENT 1

In Experiment 1, male Japanese quail were conditioned with an artificially adorned quail hen serving as the conditioned stimulus object. Because the male birds were not likely to copulate with the adorned hen at first, access to a normal sexually receptive adult female bird served as the unconditioned stimulus.<sup>1</sup> Two groups of subjects were tested. For subjects in the experimental group, exposure to the adorned quail hen was paired with access to the normal female. For birds in the control

group, these two events were presented in an unpaired fashion.

### Method

*Subjects.* The experiment was conducted in two replications. Twelve adult male Japanese quail served in each replication. The subjects in the first replication were 2 to 3 months old and were experimentally naive. Those in the second replication were 4.5 to 6.5 months old and had been used previously in studies of quail social behavior that involved 15 to 20 mating trials with normal adult female birds. The birds were hatched in the laboratory from eggs obtained from a colony of quail maintained at the University of Texas. At 30 days of age, they were removed from brooders and housed in metal quail cages (GQF Manufacturing Co.). Male birds were housed individually, and females were housed in groups of up to four per cage. Lights in the laboratory were on from 6:00 a.m. to 10:00 p.m. daily, which provided sufficient photostimulation to maintain the birds in reproductive readiness. Food (turkey grower) and water were available continuously.

*Apparatus.* All experimental procedures were conducted in large observation cages (121.9 by 91.4 by 106.7 cm). Two opposing sides and the top of the observation cages were made of plywood; the front and back walls and the floor were made of wire mesh. The front wall was hinged to provide one means of entry into the test cage. A second much smaller opening (14 by 15.5 cm) was centered along one side wall. Access through this opening was controlled by a vertically sliding opaque panel. This doorway opened to a two-compartment trolley that could be rolled back and forth on casters along the outside of the test chamber wall. Each compartment of the trolley was 11.5 cm deep and had the same width and height as the doorway so that only one compartment could be lined up with the doorway at a time. The first compartment contained an adult quail hen restrained behind a chicken-wire screen. The hen was adorned with a bright orange feather attached near each of its shoulders so that the feathers extended back at about 45°. The orange feathers were commercially available chicken feathers that had been dyed day-glow orange. They were cut to about 9 cm and were attached to the quail hen with Velcro® tabs. (A hard Velcro tab was glued to the orange

<sup>1</sup> The adorned quail hen is identified as the "conditioned stimulus" and the normal female quail is identified as the "unconditioned stimulus" for expository convenience only. We recognize that each type of female is a complex stimulus that may be partitioned into conditioned and unconditioned stimulus features for purposes of theoretical analysis (see discussion of Experiment 2 and general discussion).

feather, and a soft Velcro tab was glued to the shoulders of the female quail.) The orange feathers were removed when the hen was in its home cage.

The second compartment of the trolley contained a normal unrestrained sexually receptive adult female quail. When the second compartment was lined up with the doorway to the test arena, no barrier existed between the normal quail hen and the male subject bird, thus permitting the male to copulate with the female.

The floor of the test arena was marked in nine equal-sized zones. One of these was directly in front of the doorway to the trolley compartments. Approach to the stimulus compartments was observed by an experimenter standing in front of the cage using a time-sampling procedure. A soft auditory prompt provided a signal at 1-s intervals. Whether the observed subject was in or out of the zone in front of the stimulus doorway at the moment of successive occurrences of the auditory prompt was recorded for the duration of exposure to the adorned quail hen.

*Procedure.* In both replications, the birds were tested in two groups. Each group was housed in the observation cages during alternate 24-hr periods. While males of one group were in the observation cages, males in the other group were housed in the colony cages. Around noon each day, the subjects were exchanged, with birds that had been in the observation cages moved to the colony cages and vice versa. This procedure was started 4 days before any experimental treatments to habituate the birds to the test cages and to the alternate housing procedure. Experimental treatments were conducted each day mid-morning and mid-afternoon. With the alternating housing procedure, successive experimental sessions for a given subject were alternated between morning and afternoon.

The subjects received a mating trial in the test cages on each of 2 successive days after initial habituation. For each of these trials, an adult female bird was introduced into the male's chamber through the hinged front wall of the chamber, and the birds were permitted to interact for 5 min. Starting the next day, subjects in the first replication received four daily treatment trials. For birds in the experimental group ( $n = 6$ ), each trial was started by raising the door to the trolley compartments. This resulted

in exposure to the adorned quail hen that had been placed in the first compartment earlier. After 30 s, the trolley was shifted, bringing the unrestrained normal female's compartment in line with the doorway. The male subject was then given 5 min to interact with the normal quail hen. Five minutes is usually long enough for completion of copulation (Schein, Diamond, & Carter, 1972). The doorway was then closed, and the hens were removed until the next conditioning trial.

Subjects in the control group ( $n = 6$ ) received the same type of presentation of the adorned quail hen as birds in the experimental group. After the 30-s exposure to the adorned hen, the second stimulus compartment was moved in line with the doorway for 5 min, but the second compartment was empty. For control subjects, the normal unrestrained female quail was introduced into the test cage through the hinged front wall of the chamber about 2 hr before exposure to the adorned female. Thus, for control subjects, exposure to the adorned female was not paired with access to the normal hen.

Following conditioning, each subject received a test trial in which it was permitted to copulate with the adorned hen. For this trial, the adorned hen was introduced through the hinged front wall of the test arena and was permitted to remain in the test cage for 5 min. The latency of the first grab response and the frequency of grab, mount, and cloacal contact responses were recorded.

The second replication was conducted the same way as the first except that five instead of four conditioning trials were conducted prior to test of copulation with the adorned female. Similar results were obtained in the two replications; therefore, the data were combined for presentation. The data of subjects that never copulated with the normal quail hen during the conditioning phase of the experiment were discarded. There were 3 such birds in the control group in the first replication and 1 each in the experimental and control groups in the second replication. This left 11 subjects in the experimental group and 8 in the control group.

### Results

The percentage of time subjects were observed in the floor zone closest to the doorway to the stimulus compartments is summarized in Figure 1 for each group of subjects. The

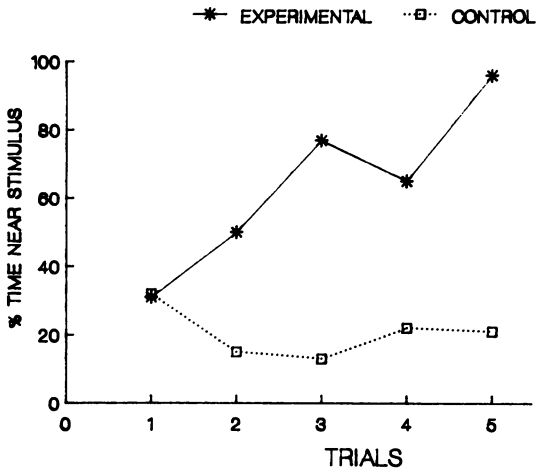


Fig. 1. Mean percentage of time experimental and control groups were observed near the adorned female during conditioning trials in Experiment 1. Data for all subjects are presented for Trials 1 through 4. For Trial 5, only data for the second replication are presented, because subjects in the first replication only received four trials.

conditioning procedure quickly resulted in approach of the adorned quail hen by birds in the experimental group. The two groups spent about 30% of the 30-s stimulus exposure time near the adorned female on the first trial. By the third trial, experimental subjects increased their time near the adorned female to a mean of 77%. In contrast, responding among control subjects declined slightly.

The approach scores of individual subjects on each conditioning trial are presented in Table 1. Three birds in the experimental group showed little evidence of conditioning. One of these (1507) was observed near the adorned hen less than 10% of the time on each trial; Birds 1323 and 1494 were observed near the adorned hen 80% and more of the time starting with the first conditioning trial. More orderly acquisition functions were observed in the other 8 subjects. None of the birds in the control group showed any systematic evidence of acquisition of approach to the adorned female. Most of the control subjects spent very little time near the adorned hen on all trials. Control Bird 1333, however, spent more than 75% of its time near the adorned female on every trial.

Although no systematic measurements of the behavior of the birds were made in the absence of the conditioned stimulus, casual observation indicated that the birds did not remain near

Table 1

Approach scores (%) of individual subjects during conditioning trials of Experiment 1.

Subject	Trials				
	1	2	3	4	5
<b>Experimental group</b>					
1507	0	0	0	7	
1508	20	83	83	93	
1509	57	93	97	97	
1530	40	3	70	83	
1531	17	33	93	70	
1532	28	10	93	70	
1323	80	83	90	97	97
1340	0	0	87	0	97
1370	23	77	48	0	97
1494	80	83	93	97	93
1364	0	87	93	97	97
<b>Control group</b>					
1537	0	0	0	0	
1504	0	0	0	13	
1534	0	0	0	0	
1333	77	90	87	93	97
1366	60	0	0	0	0
1413	0	0	0	0	0
1368	20	30	17	73	10
1337	97	0	0	0	0

the doorway to the stimulus compartments when the door was in the lowered position (see also Domjan *et al.*, 1986). After a few conditioning trials, when the door was raised revealing the adorned female bird experimental subjects quickly ran over to her and often pecked at her through the separating wire screen. Such behavior usually was not observed among birds in the control group.

Results of the test of copulation with the adorned hen are summarized in Figure 2. Birds in the experimental group made on average many more grab, mount, and cloacal contact responses directed toward the adorned female than did birds in the control group. Only 1 (1340) of the 11 experimental birds failed to make sexual contact with the adorned female. Eight experimental birds were observed to make more grab and mount responses than any of the control subjects, and these 8 birds were observed to make more cloacal contact responses than all but 1 of the control subjects. All control subjects made sexual contact with the adorned hen, but the level of their activity was much lower than that of the experimental subjects. Mann-Whitney *U* tests (two-tailed) indicated that the difference between the ex-

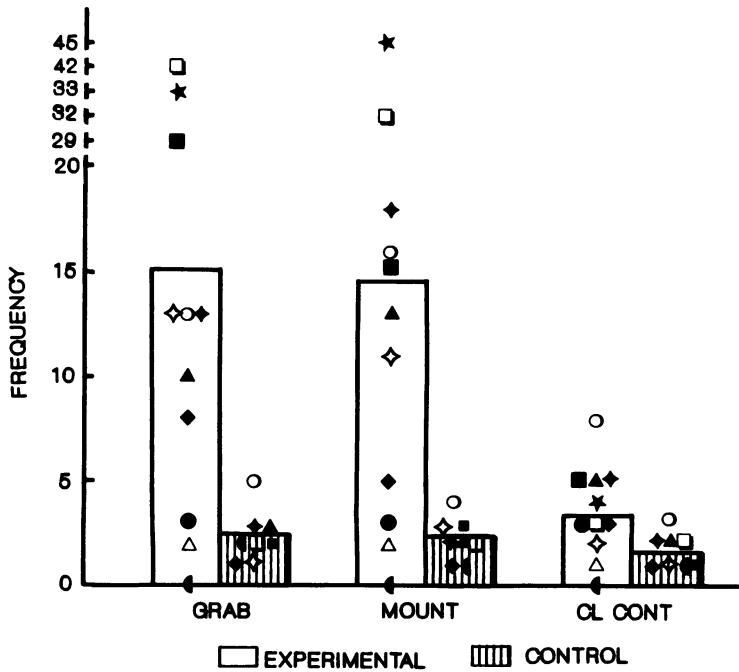


Fig. 2. Frequency of grab, mount, and cloacal (CL) contact responses observed for experimental and control groups during the postconditioning test with an unrestrained adorned female in Experiment 1. Bars depict group means. Within each group, different symbols depict the performance of different subjects.

perimental and control groups was significant for each aspect of copulatory behavior (smallest  $U = 16.5$ ,  $p < .05$ ).

### Discussion

The acquisition of approach behavior in experimental but not control subjects illustrates the conditioning of an appetitive component of sexual behavior. This result confirms previous demonstrations of sexual approach conditioning in male Japanese quail (Domjan et al., 1986). The conditioning procedure employed also increased grab, mount, and cloacal contact consummatory sexual responses directed toward the adorned female quail. This outcome provides the first clear demonstration that consummatory sexual responses can also be conditioned. Previous studies with quail (Domjan et al., 1986; Farris, 1967) probably failed to find conditioning of consummatory sexual behavior because the conditioned stimuli used (localized lights and a buzzer) did not provide supporting stimulation necessary for occurrence of sexual contact responses. The importance of the nature of the conditioned stimulus

is considered further in the subsequent experiments.

Access to a normal adult female quail was the operational "unconditioned stimulus" in our studies. The fact that experimental subjects responded to the adorned hen significantly more than control subjects did indicates that pairing exposure to the adorned hen with access to a normal female quail was important for acquisition of approach and sexual contact responses. However, we do not know what aspect of access to the normal adult female quail was critical. Exposure to the visual features of the normal hen or just to its calls might have been sufficient. Alternatively, various aspects of tactile contact and copulation with the normal hen might have been important. Additional research is necessary to decide among these possibilities.

Zamble et al. (1985) obtained evidence of sexual conditioning in male rats if the subjects were exposed to a receptive female but not allowed to copulate with her, but did not obtain evidence of conditioning in subjects that were permitted to copulate to ejaculation. Subjects

in the present study made cloacal contact with the normal female bird on each conditioning trial, indicating that copulation does not preclude obtaining evidence of sexual conditioning in Japanese quail. Perhaps the functional unconditioned stimulus for sexual conditioning is different for rats and quail. Differences in the response measures and conditioned stimuli used in the rat and quail studies may also have been responsible for the contrasting results.

## EXPERIMENT 2

Experiment 2 was conducted to identify the functional features of the conditioned stimulus used in Experiment 1. A live quail hen adorned with bright orange feathers is a complex stimulus. Responding to the adorned hen may be controlled by movement cues, vocalizations, visual appearance of certain body parts, the orange feather adornments, or combinations of such stimuli. In Experiment 2, subjects were tested with inanimate components of the adorned hen stimulus complex. The stimulus variations were introduced successively. The test series was initiated after an initial test phase in which no change in response to the adorned females was observed with repeated testing, suggesting that approach behavior conditioned to an adorned hen does not extinguish quickly.

Prior research on stimulus features important in the control of the social behavior of male quail indicated that male birds identify female quail primarily on the basis of static visual cues provided by the head and neck of females (Domjan & Nash, 1988). Experiment 2 evaluated whether static visual cues of the head and neck were also important in controlling conditioned approach to the adorned female quail.

### *Method*

*Subjects.* The 5 subjects of the first replication of Experiment 1 that had shown orderly acquisition of conditioned approach behavior (Birds 1508, 1509, 1530, 1531, and 1532) served in Experiment 2. Four test trials were conducted each day, arranged in two blocks of two trials each. For each trial, the first stimulus compartment was aligned with the vertically sliding door. The trial started when the door to the stimulus compartment was raised

and ended when the door was lowered 30 s later. For one trial in each block, the stimulus compartment was empty. For the other trial in each block, the stimulus compartment contained a quail hen or other stimulus adorned with the bright orange feathers. The order of these stimulus-present and stimulus-absent trials was counterbalanced across subjects and trial blocks. The empty-compartment tests were conducted to evaluate the extent to which approach behavior was controlled simply by the raising of the door to the stimulus compartments. The two trials within a trial block were always separated by at least 30 min and the two trial blocks within each day were separated by about 2 hr.

During the first 10 blocks of trials, subjects were tested with the same kind of live adorned female quail as they had been exposed to during conditioning trials. These tests served to document the stability of conditioned approach to the live adorned hens.

After we found that responding to the adorned hens did not extinguish with repeated testing, the subjects were tested with a variety of other stimuli. Each stimulus was tested in two successive trial blocks. The first test series was conducted to determine the importance of auditory, olfactory, and movement cues. The subjects were tested with stationary taxidermically prepared models of female quail that were adorned with the bright orange feathers in the same manner as the live female quail. The models were mounted in a standing posture, similar to the position of the live birds that had been used during conditioning trials. During the second test series, subjects were tested with the bright orange feathers mounted at 45°, 1 cm apart, on the top of a block of wood (5 by 3.4 by 3.7 cm). With this arrangement, the feathers protruded at an angle and height similar to their position on a live female bird. The third test series was conducted to evaluate the possibility that approach behavior was controlled by the orange feathers in combination with cues provided by the head and neck of a quail hen. For this test series, the wood block containing the orange feathers was placed behind a taxidermically prepared model of a female quail head with about 5 cm of neck feathers mounted on a vertical wooden dowel at about the same height as a normally standing quail. During the last test series, a live female quail adorned with the orange feathers

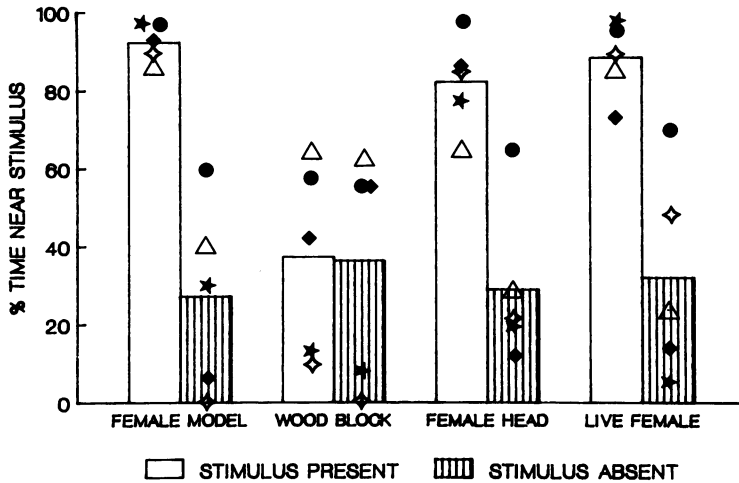


Fig. 3. Percentage of time subjects in Experiment 2 were observed near the stimulus compartment during test trials involving the presence and absence of a taxidermically prepared female model adorned with orange feathers, a wood block adorned with orange feathers, an adorned wood block placed behind a female head and neck model, and a live adorned female. Bars represent group means, and each symbol depicts the performance of an individual subject. Each data point represents the mean of two test trials.

was presented to confirm that responding to such a stimulus had not deteriorated during the course of the experiment.

### Results

During the first phase of the experiment, when the birds were tested repeatedly with a live adorned quail hen and an empty stimulus compartment, each subject consistently showed more approach behavior when the adorned hen was present than when the female bird was absent. For example, the mean approach scores of individual birds during the last two trials with the adorned hen were 90%, 96%, 92%, 75%, and 90% ( $M = 89\%$ ). The approach scores of these subjects during the last two trials with an empty stimulus compartment were 46%, 50%, 30%, 17%, and 76%, respectively ( $M = 44\%$ ). These scores were not systematically different from the approach scores of the subjects during the first two trials with an empty stimulus compartment (0%, 60%, 72%, 46%, and 26%, respectively;  $M = 41\%$ ).

The results of tests with various kinds of models, and with a live adorned female quail at the end of the experiment, are presented in Figure 3. During the first test series (when subjects were tested with a taxidermically prepared female quail adorned with the orange feathers), every subject spent more time near the stimulus compartment when the model

quail was present than when the model was absent. In addition, the adorned model quail supported as much approach behavior ( $M = 92.4\%$ ) as had been observed earlier with the live adorned quail hen. In contrast, the orange feathers by themselves did not support any perceptible approach behavior. The mean approach score during tests with the adorned wood block was only 37.4%; the mean approach to the empty stimulus compartment during this test series was 36.4%.

Placing a model of a female quail's head and neck in front of the adorned wood block resulted in recovery of the approach behavior ( $M = 82.4\%$ ). During the test series with the head and neck model in front of the block of wood, every subject again spent more time near the stimulus compartment when the stimulus was present than when it was absent. Similar results were obtained when subjects were tested with a live adorned female at the end of the experiment.

### Discussion

These results suggest that the approach behavior conditioned in Experiment 1 was controlled by the bright orange feathers in combination with visual cues provided by the head and neck of the female quail. Although vocalizations, olfactory cues, and movement stimuli may have helped to support the conditioned

approach behavior, these other stimulus features were not necessary. Furthermore, removal of these other sources of stimulation did not disrupt the approach response. As much responding occurred to models that contained the critical static visual cues as occurred to live adorned female quail. Of course, other types of tests may be more effective in revealing a contribution of nonvisual or movement stimuli.

In other experiments, male Japanese quail have been observed to become conditioned to approach a small localized visual cue (illumination of a pecking key, for example) when that stimulus was paired with access to a sexually receptive female (Domjan *et al.*, 1986). Those results suggest that stimuli do not have to include female head and neck visual cues for the occurrence of sexual conditioned approach behavior (see also Experiment 3, below). The orange feathers used in the present study probably did not elicit approach behavior when presented alone because they had been presented with female-related visual cues during the conditioning trials. This method of stimulus presentation may have resulted in the formation of a configural cue consisting of the normal feathers of the head and neck of female quail and the added orange adornments.

In considering the results of Experiment 2, it is important to keep in mind that the approach behavior of the subjects could not have been stimulated simply by the presence of visual cues of a female's head and neck. Had those cues been sufficient, subjects in the control group of Experiment 1 also would have shown substantial approach behavior. The fact that control subjects did not come to approach the adorned female quail suggests that pairing exposure to an adorned quail hen with access to a normal female was important for the development of the approach behavior.

The adorned female birds used in Experiment 1 contained the head and neck visual cues that have been shown previously to be sign stimuli sufficient to elicit approach and copulatory behavior in male Japanese quail (Domjan, Greene, & North, *in press*; Domjan & Nash, 1988). The fact that very little approach behavior occurred in control subjects (or in experimental subjects at the start of conditioning) suggests that the presence of the orange feathers discouraged the usual affiliative responses elicited by female conspecifics. The subsequent development of approach be-

havior in birds in the experimental group may have reflected loss of the disruptive effects of the orange feathers.

This loss may have occurred simply through stimulus exposure or habituation, although that seems unlikely because subjects in the control group received equal exposure to the adorned female stimulus. A more tenable hypothesis is that the disruptive effects of the orange feathers became counterconditioned through association with access to a normal quail hen. According to this interpretation, conditioning made the orange feathers less likely to disrupt approach and copulatory behavior elicited by species-specific visual cues provided by the head and neck of female quail.

### EXPERIMENT 3

The results of Experiment 2 indicated that an important component of the stimulus complex controlling conditioned approach (and presumably copulatory) behavior directed toward an adorned female quail involves the distinctive visual features of the hen's head and neck. These species-specific cues may have become a critical part of the stimulus complex controlling behavior directed toward the adorned female simply because they were present during the conditioning trials. Alternatively, the species-specific cues of a hen's head and neck may be necessary for occurrence of conditioned sexual contact behavior in male Japanese quail.

Experiment 3 was conducted to determine whether approach and copulatory behavior could become conditioned to stimuli that did not include species-specific features of a female quail. The conditioned stimulus used in Experiment 3 was a small yellow stuffed toy dog. It was similar in size to a female quail and was mounted in a similar posture, but had few, if any, quail-like features. The conditioning procedure was similar to that of Experiment 1. Exposure to the toy dog served as a signal for access to a normal female quail for subjects in the experimental group and was presented unpaired with this unconditioned stimulus for subjects in the control group.

#### *Method*

*Subjects.* Thirteen adult male Japanese quail were hatched and raised from eggs obtained from birds maintained in the Department of



Psychology at Cornell University. At 4 to 5 weeks of age, they were removed from brooders and housed individually in wire-mesh cages. Before serving in the present experiment, the subjects were used in a pilot study of sexual conditioned approach behavior in which independent groups received signaled or unsignaled access to a live normal female quail. The signal was a complex stimulus consisting of auditory and spatial cues and visual exposure to a live female quail. Only birds that showed copulatory behavior in this earlier study were selected for the present experiment. Subjects that served in the unpaired control group in the pilot study were assigned to the experimental group in Experiment 3, and those that had served in the paired experimental group were assigned to the control group in Experiment 3. Reversing the group assignments in this manner ensured that any conditioned approach behavior that was observed in Experiment 3 could not be attributed to the previous experimental history of the subjects.

**Apparatus.** The same test chambers that had been used in Experiments 1 and 2 were used in Experiment 3. In place of an adorned female bird, a stuffed toy dog (a Pound Puppy® by Tonka) was used as the conditioned stimulus. The toy measured about 14 cm from the base of the tail to the tip of the nose. It had a bright yellow terry cloth surface, a thin black collar, black nose button, and white eyes with small black pupils. The dog's neck was propped up with 5.5 cm of stiff wire, so that its head was about the height of a resting female quail's head. The dog was positioned in the stimulus compartment facing the test chamber at 45° on each conditioning trial so that both its front and side were visible.

**Procedure.** The procedure was the same as that of Experiment 1 in all unspecified respects. Each subject received one trial per day for 7 days. Trials were conducted alternately in mid-morning and mid-afternoon, starting with an afternoon trial. About 90 min before a conditioning trial, birds in the control group ( $n = 5$ ) received access to a sexually receptive quail hen for 5 min. The hen was placed in the test arena through the hinged front wall of the chamber. At the start of a conditioning trial, the door to the trolley compartments was raised, revealing the toy dog behind a wire screen. After 30 s, the trolley was shifted, bringing the second compartment in line with

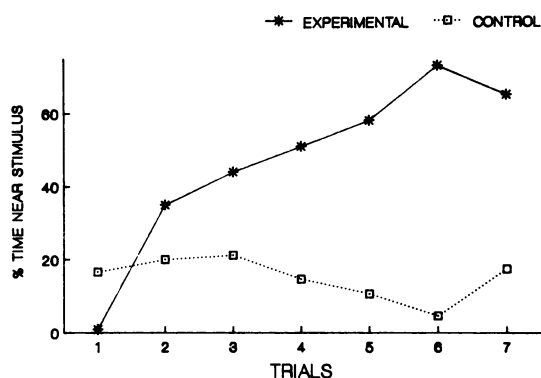


Fig. 4. Mean percentage of time experimental and control groups were observed near the toy dog stimulus during conditioning trials in Experiment 3.

the doorway for 5 min. For birds in the experimental group ( $n = 8$ ), the second compartment contained an unrestrained sexually receptive adult quail hen. For birds in the control group, the second stimulus compartment was empty.

On the morning after the seventh conditioning trial, each subject was given a test trial. Just prior to the trial, the subject was removed from its test chamber while the toy dog (mounted on a wooden platform) was placed in the center of the test cage facing the door to the trolley compartments. The male bird was then placed back in the test arena through the hinged front wall of the chamber and was allowed direct access to the toy dog for 5 min. (This direct access test was conducted with the toy dog placed in the center of the test arena to facilitate observation of interactions with the stimulus object.) The test trial was recorded on videotape for later analysis.

### Results

The subjects in the experimental group showed orderly acquisition of conditioned approach behavior over the course of the seven conditioning trials. Mean approach scores for each group of subjects are displayed in Figure 4, and the data of individual subjects are presented in Table 2. Two subjects (1674 and 1678) showed systematic fluctuations in performance, with lower approach scores on odd-numbered trials than on even-numbered trials. Odd-numbered trials were conducted in the afternoons after the mid-day movement of the birds from their home cages to the test cages (see procedure, Experiment 1); even-num-

Table 2

Approach scores (%) of individual subjects during conditioning trials of Experiment 3.

Sub- ject	Trials						
	1	2	3	4	5	6	7
<b>Experimental group</b>							
1627	7	80	70	57	67	70	77
1674	0	13	0	23	7	53	27
1676	0	7	0	10	63	29	73
1678	0	13	0	7	0	53	0
1682	0	57	93	97	97	100	94
1685	0	30	90	100	97	97	100
1689	0	80	97	97	100	100	100
1691	0	0	0	17	33	83	50
<b>Control group</b>							
1684	63	30	63	30	23	0	37
1688	0	47	23	43	10	0	0
1692	0	3	10	0	0	0	0
1628	0	10	3	0	0	13	50
1672	20	7	7	0	20	10	0

bered trials were conducted in the morning, after the birds had been housed in the test arena overnight. Birds 1674 and 1678 may have been disrupted more than the other birds by being moved from their home cages to the test cage. Overall, acquisition was somewhat slower in this experiment than in Experiment 1. Even so, mean approach scores by the last 2 days of acquisition were 73% and 65%, respectively, for birds in the experimental group, and these values were much higher than approach scores of birds in the control group.

Four birds in the control group showed inconsistent and low levels of approach behavior throughout conditioning. Bird 1684 showed a high level of performance initially (63%), perhaps due to its prior experimental history, but its approach behavior also ended up consistently below 40%.

During the postconditioning test in which the toy dog was placed in the middle of the test arena for 5 min, little evidence of behavior elicited by the presence of the stimulus was observed. Only 2 birds in the experimental group (1627 and 1682) showed any orientation toward the toy dog, and neither of them made any contact with the dog. Thus, none of the consummatory responses of grab, mount, and cloacal contact were observed in response to the toy dog.

Using the videotape records of the test per-

formance of the birds, we also measured the amount of time each bird spent in the middle 1/4th section (1,238 cm<sup>2</sup>) of the test arena that contained the toy dog. Only 4 birds ever stepped into this central area. One of them was a control subject (1628) that briefly stepped into the central area once while pacing, spending just 0.5 s there during the 5-min test. The other 3 birds were from the experimental group. Two of these birds (1627 and 1678) stepped into the central area only once, for 3.2 s and 1.0 s, respectively. Bird 1682 entered the central area 11 times for a total of 10.7 s of the 5-min test. Thus, even this measure of behavior failed to show strong evidence of conditioning.

### Discussion

Pairings between exposure to a toy dog and access to a quail hen resulted in conditioned approach of the stimulus compartment housing the toy dog. This behavior was similar to the approach of an adorned female quail that had been observed in Experiment 1, indicating that a variety of localized stimuli can be used to support sexual conditioned approach behavior. Despite evidence that conditioning had occurred, the toy dog did not stimulate much approach or sexual contact conditioning when it was placed in the middle of the test arena. This outcome contrasts with the results of Experiment 1, in which conditioning resulted in increased copulatory behavior directed toward the conditioned stimulus object.

The failure of subjects in Experiment 3 to direct copulatory responses toward the toy dog may have been caused by the absence of quail-like features. However, another possibility is that the toy dog did not become strongly associated with access to a normal quail hen. The conditioned approach behavior may have been a response to the opening of the stimulus compartment door rather than the presence of the toy dog. Perhaps the toy dog stimulus was not as effective in overshadowing the door-opening cues as the adorned female quail had been in Experiment 1. Experiment 4 was conducted to rule out this possibility.

### EXPERIMENT 4

The subjects of Experiment 3 continued to serve in Experiment 4, and a discrimination procedure was instituted to focus conditioned approach behavior on the presence of the toy

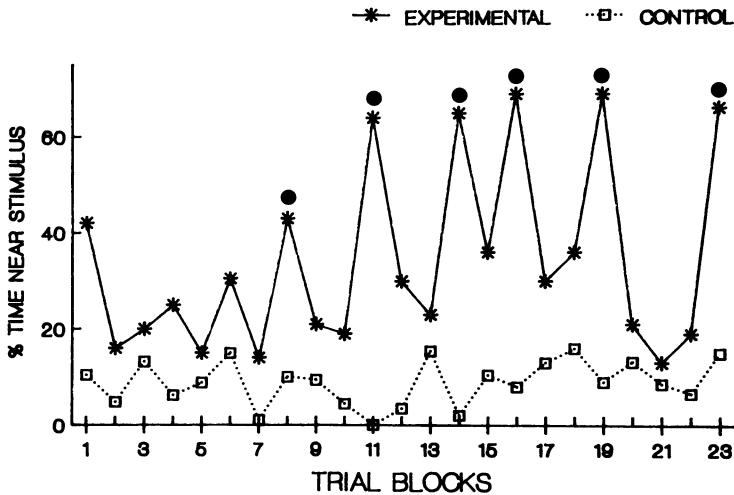


Fig. 5. Mean percentage of time experimental and control groups were observed near the stimulus compartment during Experiment 4. Data for trials without the toy dog are presented in blocks of two trials. Data for trials with the toy dog are presented in blocks of one trial; these single-trial blocks are identified by filled circles above the points.

dog conditioned stimulus. Subjects were exposed to trials in which the first stimulus compartment contained the toy dog and trials in which the first stimulus compartment was empty. Access to a receptive quail hen was provided only after exposure to the toy dog, thus extinguishing any conditioned approach behavior that might have been elicited by cues involved in opening the stimulus compartment door.

#### Method

The subjects and apparatus were the same as in Experiment 3. Experiment 4 was started 4 to 6 days after the end of Experiment 3. Subjects received two types of trials, dog present and dog absent. Trials with the dog present were conducted the same way as conditioning trials in Experiment 3. Subjects in the experimental group received exposure to the toy dog for 30 s, followed by access to a receptive adult female quail for 5 min. Subjects in the control group received access to the quail hen about 90 min before exposure to the toy dog stimulus. The assignment of subjects to groups was the same as it had been in Experiment 3. On days with a dog-present trial, no other trials were conducted.

Dog-absent trials were conducted the same way as dog-present trials except that the toy dog was absent from the first stimulus compartment when the door was raised, and a

female quail was not available in the stimulus compartment when the second compartment was moved in line with the doorway to the test arena. Dog-absent trials were run in pairs of two trials per day separated by about 90 min. Subjects received a total of 40 trials, all but six of which were dog-absent trials. Dog-present trials were conducted on Trials 15, 20, 25, 28, 33, and 40.

On the day after the 40th trial, subjects received a test session with the toy dog placed in the middle of the test arena, as in Experiment 3.

#### Results

A summary of the approach scores of both groups of subjects during dog-absent and dog-present trials is presented in Figure 5. Subjects in the control group showed little approach behavior on either type of trial throughout the experiment. Subjects in the experimental group showed substantial approach behavior during the first block of dog-absent trials ( $M = 42\%$ ) but decreased their approach to the empty stimulus compartment as training continued.

The long string of dog-absent trials at the start of the experiment seemed to cause some disruption of approach behavior directed toward the toy dog among experimental subjects. The mean approach score of the experimental group during the first dog-present trial in Experiment 4 was only 43%. However, ap-

proach to the toy dog quickly recovered. The mean approach score on the second dog-present trial was 64%, and mean responding remained around 67% for the remaining dog-present trials.

The discrimination between dog-present and dog-absent trials that was evident in the group means was also evident in the performance of individual subjects. For example, every subject in the experimental group responded more during each of the fifth and sixth dog-present trials than they did during the immediately preceding block of two dog-absent trials. Only 1 subject ever responded less during a dog-present trial than during the preceding dog-absent trial (Bird 1676 during the third and fourth dog-present trials).

Although the discrimination training ensured that subjects in the experimental group were responding to the presence of the toy dog as a signal for copulatory opportunity, this did not result in sexual contact responses when the toy dog was made available in the middle of the test arena during the postconditioning test. None of the subjects made any contacts with the toy dog. Two birds in the experimental group (1678 and 1685) and one in the control group (1628) showed some orientation toward the toy stimulus. Bird 1678 oriented toward the toy dog on two occasions with its back feathers erect, and Bird 1685 approached the toy dog while oriented toward it on two occasions. Bird 1628 oriented toward the dog once, with its neck stretched out toward the dog.

As in Experiment 3, using video records of the test trial, we measured the amount of time subjects spent in the central  $\frac{1}{3}$ th section of the test arena where the toy dog was positioned. Two birds in the control group (1675 and 1628) each stepped into the central section once briefly (for 0.5 s) while moving from one area of the test chamber to another. One bird (1676) in the experimental group also showed one such brief entry. Two other birds in the experimental group got close to the toy dog more often. Bird 1627 entered the middle area six times for a total of 5.7 s. Bird 1678 entered the middle area three times for a total of 2.8 s of the 5-min test.

### *Discussion*

The present results indicate that failure of birds in the experimental group to contact the

toy dog in Experiment 3 was not due to the toy being a poor signal for access to a normal quail hen. The discrimination training procedure successfully restricted conditioned approach behavior to trials on which the toy was presented. Thus, the conditioned approach response came to be elicited specifically by the toy stimulus. Nevertheless, no contact responses were made to the toy dog.

The absence of sexual consummatory responses to the toy dog contrasts with the effectiveness of artificially adorned female quail to stimulate such behavior in Experiment 1. This difference in responding could be due to any number of differences between the two types of stimuli. One possibility is that quail are not likely to direct copulatory responses to inanimate objects. This seems unlikely, however, because in recent research (Domjan *et al.*, in press) we have observed male Japanese quail to copulate normally with inanimate models that contained a female quail's head and neck when the models were presented in the same place where the subjects previously copulated with live female birds.

Another noteworthy aspect of the present results was that the approach behavior that became conditioned to the toy stimulus was most clearly evident when the toy dog was located where a sexually receptive female was to appear. When the toy dog was moved to the center of the test arena, much less approach behavior occurred. Although a few of the birds got close to the toy dog, many did not, and none of the subjects spent more than a few seconds in the middle of the test arena.

The failure of subjects to approach the toy dog in the middle of the test arena probably was not due to a tendency of Japanese quail to avoid this part of the test chamber. Subjects that had been conditioned in Experiment 1 with an adorned female quail as the cue for access to a normal female had been given a similar test of transfer of the conditioned approach behavior. At the end of Experiment 2, subjects from that experiment were tested with an adorned quail hen restrained in a clear plastic holder in the middle of the test arena. A time-sampling procedure was used to record the approach response of the male subjects. The position of each subject was observed 30 times at 3-s intervals. Subjects that previously received exposure to the adorned hen paired with access to a normal female quail spent a

mean of 84% of the observations in the middle area near the adorned hen. In contrast, subjects in the control group were observed to be in the middle area only a mean of 43% of the time (Mann-Whitney  $U = 19$ ,  $p < .05$ , two-tailed). These results indicate that male Japanese quail will approach the center of the test arena when a sufficiently attractive stimulus is located there. These results also indicate that under certain conditions subjects will approach a sexually conditioned stimulus even if that stimulus is presented away from where the subjects previously received access to a normal female quail.

### GENERAL DISCUSSION

As in other forms of species-typical behavior, reproductive behavior may be viewed as consisting of appetitive and consummatory components. The appetitive component may be assumed to include search and approach behavior, whereas the consummatory component involves copulatory contact responses. The present experiments provide evidence that both appetitive and consummatory components of reproductive behavior are susceptible to modification by conditioning procedures. Subjects came to approach an artificially adorned quail hen and a stuffed toy dog when these stimuli were paired with access to a normal female conspecific. These studies also demonstrated that a conditioning procedure can enhance species-typical copulatory responses directed toward an adorned quail hen. This finding is the first demonstration that conditioning can redirect consummatory sexual responses.

Appetitive sexual responses apparently can come under the control of a wide range of stimuli. In prior research, sexual conditioned approach behavior was observed in response to illumination of a red light bulb and illumination of a pecking key (Domjan et al., 1986). In the present studies, conditioned approach behavior was observed in response to an adorned female quail (Experiments 1 and 2) and a toy dog (Experiments 3 and 4). These results are consistent with previous suggestions that appetitive components of a species-typical behavioral sequence are "adaptable to changing situations" (Eibl-Eibesfeldt, 1970, p. 45) and characterized by "plasticity" (Tinbergen, 1951, p. 105).

Although both the adorned quail hen and

the toy dog stimuli supported conditioned approach behavior, they did not do so in the same way. Subjects approached the adorned quail even when it was placed in the test arena rather than constrained in the side stimulus compartment. In contrast, very little approach behavior occurred when the toy dog was moved to the center of the test arena.

One prominent difference between the adorned quail and the toy dog was that the toy was immobile whereas the adorned quail was alive and active. Lack of movement may have contributed to the lack of transfer of the conditioned approach behavior when the position of the toy dog was changed. Movement of a stimulus object against a stationary background should facilitate perceptual differentiation of the object from background cues and thus help ensure that the object becomes conditioned independent of the background. With an immobile object, conditioning may be more likely to accrue to a configuration of the object together with background cues. Changes in that configuration resulting from relocation of the object to a different background would result in decreased conditioned approach behavior.

In contrast to sexual conditioned approach behavior, which occurred in response to a range of conditioned stimuli, consummatory sexual responses became redirected as a result of conditioning only when an adorned quail hen signaled access to a normal female conspecific. The failure of the toy dog to support conditioned sexual contact responses reflects a limitation or constraint on the susceptibility of consummatory sexual responses to conditioning. This limitation is consistent with previous characterizations of consummatory behavior as more "rigid" (Tinbergen, 1951, p. 105) and "automatically discharged" (Eibl-Eibesfeldt, 1970, p. 45) compared to appetitive behavior.

What was the source of the limitation on the conditioning of consummatory sexual responses? One possibility is that the differences in how approach behavior became conditioned to the adorned quail and toy dog stimuli were responsible for the differences in sexual contact responses elicited by these stimuli. As was noted above, more transfer of conditioned approach behavior was observed when the adorned hen was released in the test arena than when the position of the toy dog was changed between conditioning and test trials. Approach behavior

is necessary for the occurrence of sexual contact responses. Therefore, the lack of transfer of the conditioned appetitive component of reproductive behavior may have contributed to the lack of sexual contact responses elicited by the toy dog. This interpretation implies that procedures that promote transfer of the conditioned approach behavior will also facilitate occurrence of conditioned sexual contact responses.

A second possibility is that differences in the occurrence of conditioned sexual contact responses reflected differences in what subjects learned as a result of the conditioning procedures. Conditioned copulatory behavior may have reflected the learning of an association between the conditioned stimulus and sexual contact responses (a stimulus-response association), and this association developed only when the adorned hen served as the conditioned stimulus. Perhaps some sort of "stimulus relevance" or "belongingness" principle limited the conditioning of the toy dog stimulus.

A third possibility is that subjects learned the same type of thing in the adorned quail and toy dog experiments, but to different degrees. Conditioned copulatory behavior in response to the adorned hen may have reflected stronger conditioning afforded by greater opportunity for associative mediation. The reinforcer for conditioning in the present studies was some aspect of access to a normal female quail. Thus, the reinforcer was experienced in close contiguity with visual cues of the head and neck of a quail hen. Similar female head and neck visual cues were present as part of the adorned hen stimulus but were not available as part of the toy dog stimulus. Commonality in the stimulus components of the unconditioned and conditioned stimuli in the adorned quail experiment may have resulted in stronger conditioning of the adorned quail and thus resulted in conditioned sexual contact behavior.

A fourth possibility also assumes that subjects learned the same type of thing in the adorned quail and toy dog experiments but attributes differences in outcome to performance rather than learning factors. Performance of consummatory sexual responses may require the presence of species-specific stimuli provided by a female conspecific. Male quail may copulate only in response to cues provided

by a female quail. Not all of the usual stimuli of a normal female quail may be necessary if the male is in a state of heightened sexual arousal. Nevertheless, even in this state, some female quail features may be required.

Perhaps as a result of sexual conditioning, the conditioned stimulus (be it an adorned quail or a toy dog) comes to elicit sexual arousal. This conditioned sexual arousal serves to lower the threshold for occurrence of consummatory sexual behavior. In this sexually motivated state, subjects are more likely to copulate with female quail whose stimulus features have been altered in some ways (such as by the addition of bright orange feathers). However, no amount of increased sexual arousal may be sufficient to stimulate copulation with an object such as a toy dog, which lacks all quail-like features.

According to this last possibility, the orange feathers used as adornments in Experiment 1 served two functions. First, because they were paired with access to a normal quail hen, they served as part of the conditioned stimulus complex that came to elicit increased sexual arousal. Second, they served to alter the normal appearance of a quail hen so that only subjects that were in a state of increased sexual arousal were likely to make sexual contact responses during the copulation test with the adorned female. Presumably these two stimulus functions could be separated by using one stimulus to elicit conditioned sexual arousal and another to alter the normal appearance of a quail hen. The implication is that a sexually conditioned stimulus will facilitate copulation with an adorned hen, even if the adornments are not part of the stimulus complex that elicits conditioned sexual arousal.

Finally, let us consider the implications of the present results for mate selection and sexual selection. The present studies did not include choice tests to determine whether the conditioning procedures resulted in a change in mate preference. Therefore, the implications of these studies for sexual selection can be offered only tentatively. Nevertheless, our results suggest a possible contribution of conditioning mechanisms to the evolution of heritable distinctive body features or "aesthetic traits." Regardless of the origin of distinctive body features, such features are potential conditioned stimuli. If such stimuli become associated with members of the opposite sex, the presence of these features may increase the

attractiveness of a potential mate and thereby influence mate choice and the characteristics of resultant offspring. Thus, associative mechanisms may contribute to the evolution of distinctive body features or aesthetic traits.

Suggestive evidence in support of the above hypothesis is provided by studies with zebra finches that have shown that experimentally introduced body adornments that alter the attractiveness of potential mates can influence subsequent reproductive success (Burley, 1981, 1986; Burley, Krantzberg, & Radman, 1982). In these experiments, the body adornments were colored leg bands. Certain colors increased the attractiveness of a bird to conspecifics of the opposite sex; other colors decreased a bird's attractiveness. The experiments did not explore what behavioral processes were responsible for these changes in attractiveness. However, some form of learning may have been involved, because the relative preferences for the band colors became more stable with repeated exposure to the banded birds (Burley et al., 1982).

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Received September 28, 1987  
Final acceptance May 12, 1988